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Evaluating a trait-based approach to compare natural enemy and pest communities in agroforestry vs. arable systems

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Abstract. Diversified farming systems, for example those that incorporate agroforestry elements, have been proposed as a solution that could maintain and improve multiple ecosystem services. However, habitat diversification in and around arable fields has complex and inconsistent effects on invertebrate crop pests and their natural enemies. This hinders the development of policy recommendations to promote the adoption of such management strategies for the provision of natural pest control services. Here, for the first time, we conducted a trait-based approach to investigate the effect of farming system on plant, invertebrate herbivore, and invertebrate natural enemy communities. We then evaluated this approach by comparing the results to those generated using a traditional taxonomic approach. At each of three working farms, we sampled within an agroforestry field (a diverse farming system comprising alleys of arable crops separated by tree rows), and within a paired non-diversified area of the farm (arable control field). Each of 96 sample points was sampled between 8 and 10 times, yielding 393,318 invertebrate specimens from 344 taxonomic groups. Diet specialization or granivory, lack of a pupal stage, and wing traits in invertebrates, along with late flowering, short flowering duration, creeping habit, and perenniality in plants, were traits more strongly associated with agroforestry crop alleys than the arable control fields. We hypothesize that this is a result of reduced habitat disturbance and increased habitat complexity in the agroforestry system. Taxonomic richness and diversity were higher in the agroforestry crop alleys compared to the arable control fields, but these effects were stronger at lower trophic levels. However, functional trait diversity of natural enemies was significantly higher in the agroforestry crop alleys than the arable control fields, suggesting an improved level of biocontrol, which was not detected by traditional diversity metrics. Of eight key pest taxa, three were significantly suppressed in the agroforestry system, while two were more abundant, compared to the arable control fields. Trait-based approaches can provide a better mechanistic understanding of farming system effects on pests and their natural enemies, therefore we recommend their application and testing in future studies of diversified farming systems.

Key words: *conservation biological control; functional diversity; functional traits; invertebrates; natural pest control; silvoarable; weeds.*

Introduction

Sustainable intensification of agriculture, or ecological intensification, has been proposed as a nature-based solution to meet food production demands by utilizing ecosystem services, such as natural pest control, rather than depending solely on external inputs (Bommarco et al. 2013, Garnett et al. 2013). For example, natural landscape elements and diversified farming systems have been proposed as an effective means of encouraging the predators and parasitoids (i.e., natural enemies) of invertebrate pests, which could help reduce the current reliance on pesticides for agricultural production (e.g., Landis et al. 2000, Bianchi et al. 2006, Attwood et al. 2008). Recently, however, there has been growing recognition that the responses of invertebrate natural enemies and pests to diversification are complex and depend on taxa and context, such as landscape configuration and diversity, farm management, and climate (Straub et al. 2008, Tscharntke et al. 2016, Karp et al. 2018). This results in a major obstacle for the development of policy recommendations to promote the adoption of agricultural management strategies for natural pest control. The uptake of such strategies remains very limited (Kleijn et al. 2019) and growers are sometimes fearful

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that they might exacerbate pest problems (Chaplin-Kramer et al. 2019).

One method proposed to enhance our understanding of the mechanisms and biotic processes that underpin the complex responses of invertebrate pests and their natural enemies to diversification is a functional trait-based approach (Wood et al. 2015, Jonsson et al. 2017, Perović et al. 2018). Here, biological communities are described in terms of their mean trait values or trait diversity rather than their taxonomic identities, on the premise that an individual's response to, or effect on, the environment is influenced primarily by traits such as feeding specialization, dispersal tendency and hunting mode (Perović et al. 2018). This trait-based approach has the potential to move our understanding away from context- and taxon-specific case studies to a more general, mechanistic, and predictive framework (Wood et al. 2015).

The application of trait-based approaches to agroecosystems has therefore been identified as an urgent research need (Wood et al. 2015, Karp et al. 2018, Perović et al. 2018). While trait-based approaches have been widely used to understand ecosystem functions and dynamics in plant and soil invertebrate ecology (e.g., Lavorel 2013, Pey et al. 2014, Faucon et al. 2017), recent applications suggest they can also shed light on the complexity of functional biodiversity responses to landscape composition and configuration (Martin et al. 2019), and explain the effect of natural enemies on prey suppression through functional trait diversity (Greenop et al. 2018).

A diversified farming system that is receiving revived interest in the context of ecological intensification of agriculture is agroforestry, which is loosely defined as farming with trees. For example, agroforestry is now promoted by the European Union's Common Agricultural Policy (Article 23 of Regulation 1305/2013) and by the United States Department of Agriculture (2019). This promotion is in part on the basis of evidence of improved productivity and regulating ecosystem services (e.g., Torralba et al. 2016, Waldron et al. 2017). Agroforestry systems have some ecological analogies to hedgerows, grass strips, and flower strips, but the productivity of the tree rows allows for a much greater density, and increased longevity, of perennial vegetation strips within a field. Therefore, agroforestry systems have the potential to deliver an even greater enhancement of natural enemies and suppression of invertebrate pests compared to other types of perennial vegetation strips (e.g., Collins et al. 2002, Hatt et al. 2017). However, the considerable variation in results among studies of agroforestry systems to-date suggests that effects on natural pest control could be dependent on taxon and/or context (Pumariño et al. 2015, Staton et al. 2019).

Trait-based approaches have recently been applied within an agroforestry system in France to understand the spatial patterns of plant and winter carabid beetle communities. Carabid beetle traits that were more associated with tree rows than adjacent arable crop alleys included large body size, granivorous diet, and adult overwintering, which were explained in terms of sensitivity to agricultural disturbance (Boinot et al. 2019*b*). The authors hypothesized that this could result in greater trait complementarity in arable alleys within agroforestry systems in comparison to arable fields, potentially leading to enhanced biological control of a wider range of prey taxa, including weeds. Perennial, rhizome- or stolon-spreading plant species were better able to disperse into arable crop alleys from tree rows, although weed/crop ratios were similar and nonsignificant between agroforestry crop alleys and arable control fields (Boinot et al. 2019*a*). However, this trait-based approach has not yet been applied to compare invertebrate and plant communities within agroforestry systems to those in non-diversified arable fields.

Therefore, in this study, we adopt this trait-based approach and compare it to a traditional taxonomic approach to investigate the effect of field-scale agroforestry systems vs. non-diversified arable fields on communities of plants, invertebrate herbivores and invertebrate natural enemies. We selected experimentally robust sites with well paired arable control fields, and maximized temporal replication to generate a representative data set for the main duration of insect activity during each year. We therefore sampled on 8–10 occasions over 2 yr across three working farms (see Appendix S1 for photos and further details). Each farm contained a paired agroforestry system and an arable control field, both of which were under the same management regime. This field-scale approach allowed us to realistically sample community interactions under field conditions (Kleijn et al. 2019). This is particularly important for functional trait studies, which are potentially strongly scale dependent (Wood et al. 2015).

The agroforestry systems at our study sites were all based on an innovative design, comprised of fruit trees (predominantly apple) intercropped with a cereal-based rotation. This system aims to maximize productivity and multiple ecosystem services (Smith et al. 2016) and, while they are currently rare globally, interest and uptake is increasing in the UK (Newman et al. 2018).

In this study, we aim to test the effect of farming system (agroforestry vs. arable) on (1) trait and taxonomic-identity community composition for each of three trophic levels (plants, invertebrate herbivores, and invertebrate natural enemies), (2) diversity metrics, including taxonomic richness and Shannon diversity across trophic levels and, for natural enemies, phylogenetic and functional diversity of effect traits, and (3) a series of key pest taxa with differing trait profiles.

Materials and Methods

Field sites

Three field sites, located in East Anglia and the East Midlands of the UK, were selected on the basis that each

possessed a similar type of agroforestry system and a non-diversified arable control field under the same farm management and crop rotation. This allowed us to control for confounding factors, such as management and landscape context, between farming systems as far as possible while sampling within realistic field-scale conditions. All sites were working farms; two were organic while the third was conventional and minimum-tillage. Crop rotations were based on cereals, plus oilseed rape at the conventional farm. The agroforestry fields were based on the innovative silvoarable system introduced at Whitehall Farm, Cambridgeshire in 2009 (Newman et al. 2018). In this system, arable crop alleys (24 m in width) are intercropped with 3–4 m wide tree rows, which predominantly contain apple trees on semi-dwarf rootstocks. Depending upon the farm, the agroforestry trees were planted in late 2009, early 2014, or early 2015. Further information is provided in Appendix S1.

Experimental design

Two crop alleys were sampled in the center of an agroforestry field at each site. Eight sample points were distributed at set distances from the tree row across each alley, including two points in each adjacent tree row, and were randomly staggered parallel to the tree row (Appendix S2: Fig. S1). Therefore, there were 16 sample points in the agroforestry field at each site. The same sampling arrangement was repeated in a non-diversified arable field at each site to act as a control. Therefore, across all sites, there were a total of 96 sample points. All samples were located at least 30 m from the nearest field boundary to minimize the influence of edge effects.

Samples were collected from May to October 2018, and April to November 2019. A variety of techniques were employed at each sample point to target different elements of the plant and invertebrate communities. These comprised pitfall traps to sample ground-based invertebrates, pan traps to sample aerial insects, crop assessments to count aphid numbers, and quadrats (excluding tree rows) to record non-crop plant species and their coverage. Pitfall trap capture rates are a measure of activity-density, and differed markedly between tree rows and arable crop alleys, including just 1.5 m away from the tree rows. This was probably due to the higher vegetation complexity in the tree rows reducing movement activity (Thomas et al. 2006). Pitfall trap samples from tree rows were therefore not included in the analysis, because of this apparent source of bias. Damaged traps were not included in the analysis, which amounted to 50 of 756 pitfall trap samples and 19 of 864 pan trap samples (Appendix S2: Table S3). At each site, pitfall traps were sampled 8–10 times over 2 yr, pan traps 9 times, quadrats twice (i.e., once per year), and aphid crop assessments once in July 2019. Further information on sampling methodology is provided in Appendix S2. All specimens (except Collembola in 2018) were identified to establish trophic level, which required varying taxonomic resolution (Appendix S3).

Data analysis

Three trophic levels were considered in the analysis, comprising plants, herbivorous invertebrates, and natural enemy (predator or parasitoid) invertebrates. Each taxon was assigned a trophic level based on information in the literature (Data S1). Pitfall trap data were adjusted to provide mean number of captures per day. Exploratory analysis was initially undertaken separately for pitfall and pan trap data sets; however, no consistent differences in effects of farming system on trait profiles were apparent between the sampling methods. Therefore, both data sets were analyzed together for the invertebrate community analyses (*Responses of traits vs. taxonomic-identities* and *Effect of farming system on diversity metrics*) to investigate overall effects at the trophic level, which meant that tree row data were excluded (as discussed in *Experimental Design*). Due to field sampling constraints, in some cases, pitfall and pan trap samples were collected in different months. In these cases, to simplify the data structure, pan trap samples were reassigned to the nearest pitfall trap month, which never exceeded one month and a day. All analyses were undertaken in R version 3.5.2 (R Core Team 2018).

Comparing traits to taxonomic identities.—We selected traits based on those hypothesized to underpin community responses to environmental and trophic effects (Storkey et al. 2013, Greenop et al. 2018, Perović et al. 2018), particularly in the context of agroforestry (Boinot et al. 2019*a*, *b*). Traits were not selected if they were unknown for a high proportion of specimens. For plants, five continuous and three categorical traits were selected, while seven categorical traits were selected for invertebrates (Table 1). For each trait, each taxon (e.g., species) within the associated trophic level was assigned a single trait value/category where possible, based on information in the literature (Data S1, Data S2). Categorical trait information was combined with abundance data collected from pitfall and pan traps, or quadrat cover for plants, such that the trait data set comprised the number of specimens (or percentage cover for plants) belonging to each trait category for each sample. This allowed for comparisons with the abundances of taxonomic identities. Continuous traits (in plants) were represented by community weighted means of scaled and centered trait values using the "scale" R function, following log-transformation where appropriate.

A partial redundancy analysis (pRDA) was run separately for taxonomic and trait data, for each of the three trophic levels. For invertebrates, separate taxonomic pRDAs were run using (1) order-level resolution (or class/sub-class for some non-insect invertebrates such as millipedes, see Appendix S3) and (2) the most precise taxonomic resolution in the data set. This led to eight

Table 1. Traits used in the analysis of effect of farming system (agroforestry alleys vs. arable) on community trait responses for three trophic levels.

Trophic level and trait	Trait values/categories
Plants	
Perenniality	annual/biennial, perennial
Clonality	creeping, non-creeping, part-creeping
Cotyledons	monocot, dicot
Month of first flowering	month as a continuous variable
Flowering duration	number of months (continuous variable)
Seed mass (g/1,000 seeds)	continuous variable
Height (cm)	continuous variable
Specific leaf area (SLA, mm^2/mg)	continuous variable
Herbivorous invertebrates	
Need for year-round vegetation	no requirement for year-round vegetation, some requirement, need for year-round vegetation
Herbivorous and natural enemy invertebrates	
Diet of functional life stage	generalist (consumes multiple taxonomic orders), granivore, specialist (preferred prey limited to one or two taxonomic orders)
Domain of functional life stage	broad (regularly hunts at ground level and higher on plant stems or aerially), base of plant or ground, foliar or aerial, within plant (herbivores only)
Wings	winged, part-winged (e.g., only some life stages winged or dimorphic), unwinged
Overwinter life stage (OW)	egg, immature, adult, multiple
Life cycle	no pupal stage (exopterygote), pupal stage (endopterygote)
Natural enemy invertebrates	
Hunting strategy	active, ambush and pursue, or sit and wait

Notes: Within each trait, each taxon (e.g., species) was assigned a single trait value/category where possible, using references in Data S1 and Data S2.

pRDAs. This method was chosen as pRDA allows multiple response and explanatory variables, while covariables can be "partialled out," i.e., their effects removed before the RDA is calculated. Taxa or traits were the response variables, farming system (agroforestry or arable) was the single explanatory variable, and site and month/year were partialled-out covariables. We also ran (1) trait pRDAs for herbivores and natural enemies, using month/year (as a factor) as the single explanatory variable, separately for each farming system (agroforestry vs. arable system), to explore the effect of seasonality on traits in each farming system, and (2) pRDAs in the agroforestry system only for invertebrates (because three sites were available), with distance from tree row as the single explanatory variable, to explore spatial effects. All response variables were chord-transformed to account for the high proportion of zeros (Legendre and Gallagher 2001). For plant pRDAs, the analysis used data from the two organic sites but not the conventional site, due to low non-crop plant cover at the latter site, probably because of herbicide use.

To compare the performance of trait and taxonomic pRDAs, adjusted R^2 values, F statistics, and P values were calculated, based on 999 permutations. The analysis was undertaken using the R package vegan (Oksanen et al. 2013).

Diversity metrics.—Studies of agro-ecosystems traditionally measure taxonomic richness and Shannon diversity, but functional trait diversity is emerging as a more meaningful alternative (e.g., Greenop et al. 2018). First, we calculated taxonomic richness and Shannon diversity for each of the three trophic levels, using vegan (Oksanen et al. 2013). The analysis used the most precise resolution available in the data set, including specimens identified to lower resolutions (e.g., order, family), because the effects of land use on order-level diversity and species diversity are similar in arthropods (Biaggini et al. 2007). We also calculated functional diversity of natural enemies based on effect traits that have been shown to play an important role in herbivore suppression (Greenop et al. 2018). These comprised hunting strategy, dietary specialism, and habitat domain (Table 1). Each natural enemy taxon was assigned a category for each trait using information in the literature (Data S1).

Phylogenetic diversity can be combined with trait information to account for potentially important overlooked traits (de Bello et al. 2017). We therefore calculated phylogenetic diversity of natural enemies using a proxy phylogenetic tree based on the classification of each taxon, using the R package ape (Paradis and Schliep 2018). As traits and phylogeny are often related and non-independent, the overlap in variation was decoupled using the decouple R function (de Bello et al. 2017). This was used along with the melodic function (de Bello et al. 2016) to calculate abundance-weighted Rao indices for functional diversity, phylogenetic diversity, and decoupled phylogenetic diversity. The latter represents the phylogenetic diversity of the natural enemy community, excluding the considered traits, and thus indicates potentially unexplored traits.

The effect of farming system (agroforestry alleys vs. arable) on each diversity metric was analyzed using mixed models in the lme4 package (Bates et al. 2015), where each richness or diversity metric was the response variable, farming system was a fixed effect and both site and month/year were random intercept effects. We also ran models (1) for individual sites, to test the influence of individual sites on the overall effects, (2) with a fixed interaction effect between sampling month and farming system, with site as a random effect, to explore patterns

in richness and diversity effects over the season, and (3) for the agroforestry system only, with distance from tree row as the single explanatory variable, to explore spatial effects. Model assumptions were inspected using residual plots as recommended by Harrison et al. (2018).

Pest and weed suppression.—The effect of farming system (agroforestry vs. arable) on the abundances of eight key pest/weed taxa was analyzed using generalized linear mixed models. Key pests were defined as those included within AHDB's field crop pest encyclopedia (AHDB 2015). Models were initially fitted with a Poisson link and inspected for overdispersion, following which a negative binomial link was fitted if necessary. Months and/or sites with very low counts were excluded from the analysis where necessary to improve model fit (Appendix S4). Farming system was the single fixed effect, with site and month/year included as random effects where they were represented by more than one level. For each response taxon, data were derived from the sampling method that had the highest capture rate for that taxon. Further information on model selection is provided in Appendix S4. We also ran models for individual sites, for those taxa analyzed at more than one site, to test the influence of individual sites on the overall results. Spatial effects within the agroforestry system were explored by running models with distance from tree row as the single explanatory variable.

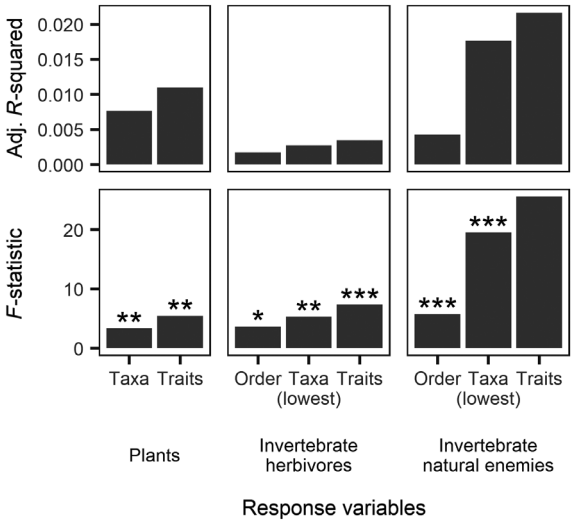

FIG. 1. Comparison of partial redundancy analysis (pRDA) performance, where taxa or traits were the response variables for each trophic level (i.e., each *x*-axis label represents a separate pRDA). The single explanatory variable in all pRDAs was farming system (agroforestry alleys vs. arable). Adjusted R^2 values represent the explanatory power of the models, while *F* statistics represent the significance of the models based on 999 permutations. Model degrees of freedom (df) were 1, residual df were 108 for plants and 651 for invertebrates. $^{***}P < 0.001$, $^{**}P < 0.01$, $^{*}P < 0.05$, $\dagger P < 0.10$.

RESULTS

Responses of traits vs. taxonomic identities

A total of 80,186 specimens representing 183 taxonomic groups were collected from the pitfall traps, while pan traps yielded 313,132 specimens from 172 taxonomic groups.

Farming system (agroforestry crop alleys vs. arable) was a better predictor of trait than taxonomic composition for all three trophic levels, according to pRDAs (Fig. 1). Improved taxonomic resolution improved predictions for natural enemies and herbivores (Fig. 1).

The taxonomic pRDAs suggested idiosyncratic responses of taxa to farming system, for example two herbivorous fly (Diptera) families strongly contrasted in their response (Fig. 2c). Of the natural enemy taxa, wolf spiders (Lycosidae) were most strongly associated with the agroforestry alleys. Ground beetles (Carabidae) showed contrasting responses, for example, *Harpalus rufipes* was strongly associated with the agroforestry alleys, while *Anchomenus dorsalis* was associated with the arable control fields (Fig. 2e).

Plant traits that were more associated with the agroforestry alleys than the arable control fields included late flowering season, short flowering duration, perenniality, and creeping habit (Fig. 2b). For herbivorous invertebrates, the need for perennial vegetation in the lifecycle, specialist diet, part-winged (e.g., dimorphic), and lack of pupal stage was positively associated with the agroforestry alleys (Fig. 2d). Similarly, natural enemy traits for granivorous or specialist diet, lack of wings and lack of pupal stage were more associated with agroforestry alleys than arable fields (Fig. 2f). However, the effect of farming system on overwintering life stage and habitat domain contrasted between trophic levels. Seasonal patterns in trait profiles were similar between farming systems (Appendix S6). There were no apparent spatial effects within the agroforestry alleys on invertebrate taxa or traits (Appendix S7: Table S1).

Effect of farming system on diversity metrics

Taxonomic richness and Shannon diversity were higher in the agroforestry alleys than the arable control fields for all trophic levels, but exhibited a "pyramid" pattern with stronger, significant effects at lower trophic levels, and a nonsignificant response for natural enemies (Fig. 3). Phylogenetic diversity of natural enemies was also not significantly different between agroforestry alleys and arable fields, but functional diversity of natural enemy effect traits, based on dietary specialism, hunting strategy and habitat domain, was significantly higher in the agroforestry alleys than the arable fields (Fig. 4). Decoupled phylogenetic diversity was not significantly different between agroforestry alleys and arable fields, indicating that important trait information was not overlooked in the functional diversity metric (Fig. 4). There were few clear seasonal differences between farming systems, although Shannon and phylogenetic diversity of natural

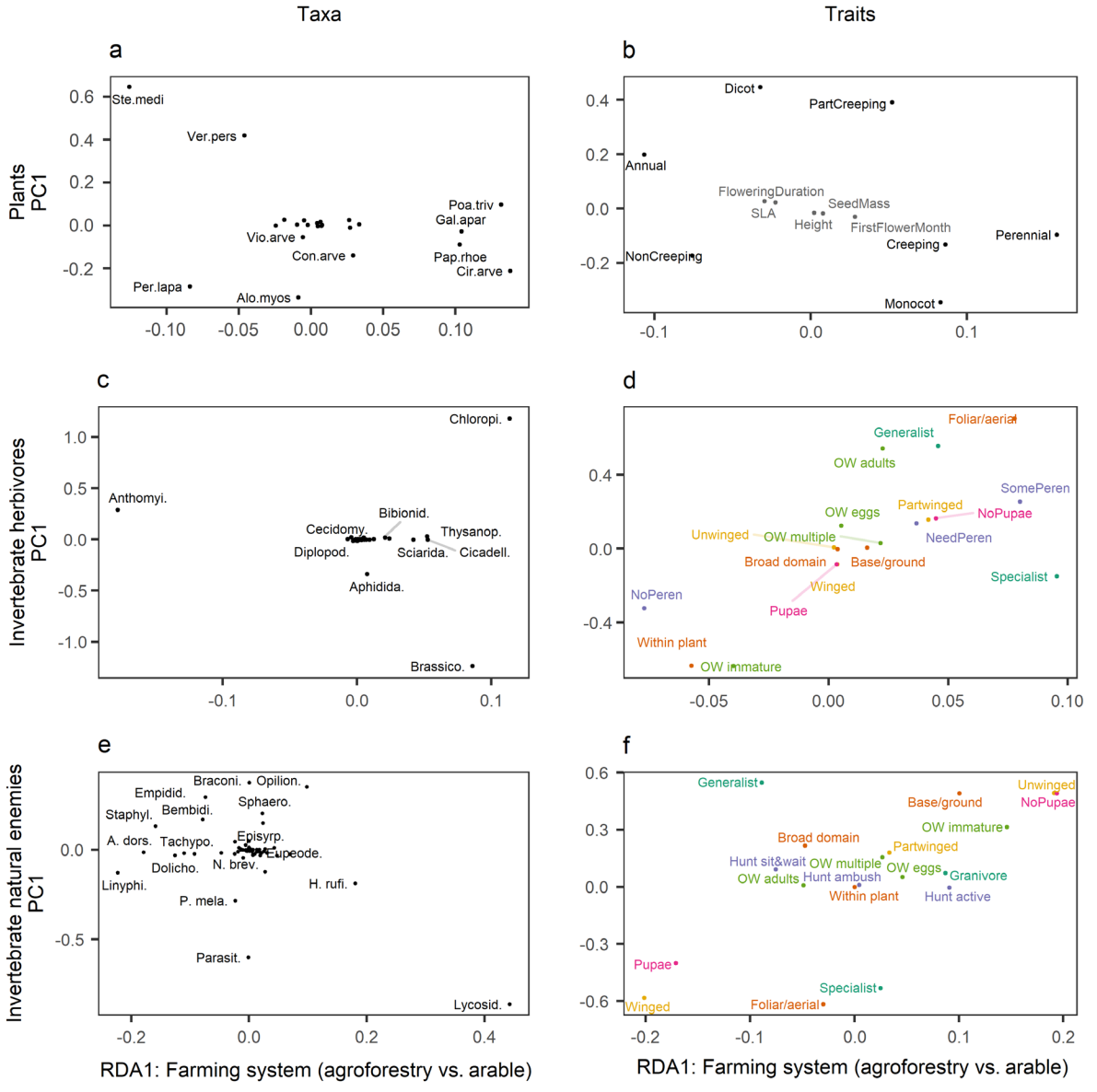

FIG. 2. Partial redundancy analysis of taxa and traits (each column), for each of three trophic levels (rows). Farming system (agroforestry alleys vs. arable) was the single explanatory variable, therefore higher *x*-axis values represent stronger association with agroforestry alleys relative to the arable system. Site and month/year were "partialled out" covariates. Trait labels correspond to Table 1. Gray labels in Fig. 2b represent continuous traits, which are on a different scale from the categorical traits (in black). Labels in Fig. 2d and f are color coded by trait category. Only the most abundant taxa are labelled. See Appendix S5 for species' abbreviations.

enemies was greater in the agroforestry alleys early in the season, relative to the arable fields (Appendix S8).

The effects of farming system on diversity metrics were reasonably consistent at the site level. At all sites, Shannon diversity of plants, herbivores, and pooled invertebrates was higher in the agroforestry alleys than the arable fields, while only one site showed a different response for taxonomic richness (Appendix S9). Similarly, functional diversity of natural enemies was higher at all three sites in the agroforestry alleys than the arable fields (Appendix S9). Within the agroforestry system, greater distance into the crop alleys slightly but significantly decreased Shannon diversity of herbivores, and taxonomic richness of pooled invertebrates, herbivores, and plants (Appendix S7: Table S2, Fig. S1).

Pest and weed suppression

The effect of farming system on the abundance of arable pests and weeds varied by taxon (Fig. 5). Three taxa were

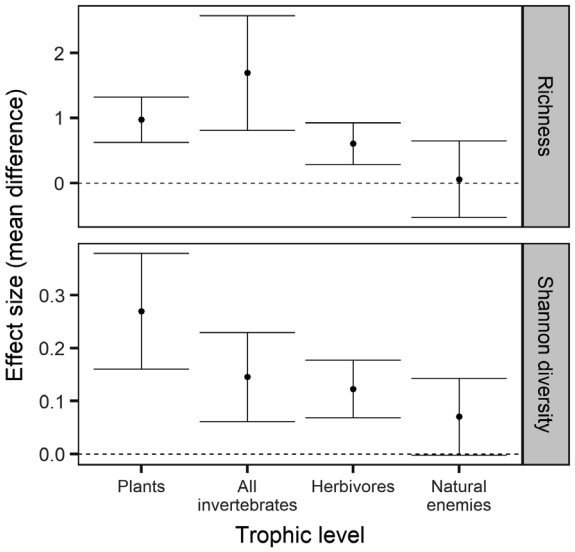

FIG. 3. The effect of farming system (agroforestry alleys vs. arable) on taxonomic richness and diversity for each trophic level, according to mixed model outputs where farming system was the single fixed effect, with site and month/year as random effects. Effect sizes are shown with 95% CI. The area above the dashed line represents higher values in the agroforestry alleys than the arable system. "All invertebrates" represent herbivores, natural enemies, and others, e.g., detritivores. See Appendix S4 for further information.

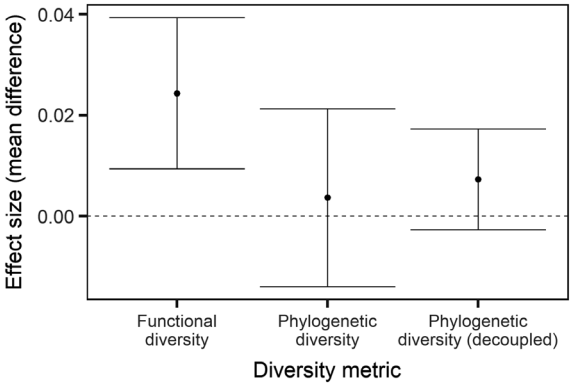

FIG. 4. The effect of farming system (agroforestry alleys vs. arable) on functional and phylogenetic diversity for natural enemies, based on mixed models as described at Fig. 3. Effect sizes are shown with 95% CI. The area above the dashed line represents higher values in agroforestry alleys than the arable system. See Appendix S4 for further information.

significantly suppressed in agroforestry compared to the arable fields. Of these, root flies (Diptera: Anthomyiidae) were consistently suppressed in the agroforestry system at all three sites (Appendix S9), with an overall reduction of 38%. A subsample of over 500 root flies was identified to species level; the dominant species was *Delia platura*, which represented over 90% of specimens at each site. Pollen beetles *Brassicogethes* spp. and wheat stem sawfly *Cephus pygmaeus* were also significantly suppressed in the agroforestry system, by 57% and 37%, respectively, but

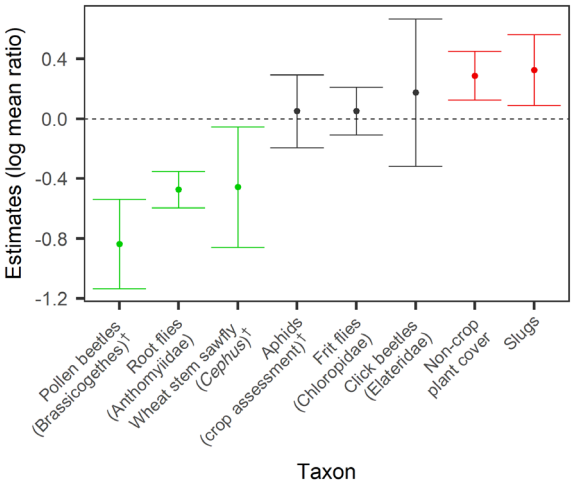

FIG. 5. The effect of farming system (agroforestry vs. arable) on the abundances of arable pests and weed coverage, derived from negative binomial generalized linear mixed models. Estimates are shown with 95% CI. The area above the dashed line represents higher abundance/cover in the agroforestry than the arable system. Taxa marked with a dagger † were only analyzed at one site as they were either scarcely recorded at the other sites, or in the case of pollen beetles, are a pest of oilseed rape, which was only grown at one site during the study period. Further outputs are provided in Appendix S4.

could only be analyzed at one site. A further three taxa, comprising grain aphid *Sitobion avenae* counts on wheat at one site, frit flies (Diptera: Chloropidae), and click beetles (Coleoptera: Elateridae), did not significantly differ in abundance between the agroforestry and arable systems, with different responses among sites (Appendix S9). Slug abundance was 39% higher in the agroforestry crop alleys than the arable fields, which was significant at both sites analyzed. The effect of farming system on non-crop plant cover differed among the two sites in which plant cover was recorded (Appendix S9), but overall was 27% higher in the agroforestry alleys than arable fields. Spatial effects of pest abundance within the agroforestry fields were weak, with significant effects limited to an increase in wheat stem sawfly abundance with distance from tree row (Appendix S7: Table S3).

DISCUSSION

Trait profiles in the agroforestry crop alleys were significantly different to the arable fields at all three trophic levels, with improved model performance compared to taxonomic identities for all trophic levels. We also found greater taxonomic richness and Shannon diversity in the agroforestry crop alleys, relative to the arable control fields, with stronger effects at lower trophic levels. Significant effects on natural enemy diversity were only detected using functional trait analyses. The effect of farming system on pest/weed abundance differed by taxon, which suggests that pest control issues in agroforestry systems differ to those in arable systems.

Interpreting functional biodiversity using a trait-based approach

For plant traits, we found that perenniality, creeping habit, and late and brief flowering were more associated with the agroforestry alleys relative to the arable fields. Although replication for plant data was limited to the two organic sites, this finding is well supported by ecological theory. In particular, the CSR (competitive, stress tolerant, ruderal) classification predicts that ruderal plant communities, characterized by short lifespan, rapid growth and flowering, and reliance on seed dispersal, are adapted to higher disturbance environments (Grime 1977). The plant community in agroforestry alleys is therefore less similar to a ruderal community and shows more characteristics that are expressed in competitive communities, reflecting the lower disturbance that occurs in these systems resulting from the presence of permanent vegetation strips.

For invertebrate communities, we found evidence of more diet-specialized herbivores and natural enemies in the agroforestry alleys relative to the arable fields. We hypothesize that this is because specialist invertebrates are more sensitive to local and landscape simplification than generalists (Tscharntke et al. 2012, Gámez-Virués et al. 2015), probably due to the lower dispersal ability and home ranges of specialists, although the strength of the effect varies according to scale (Tscharntke et al. 2005, Chaplin-Kramer et al. 2011). Granivorous natural enemies, which comprised carabid beetles such as *Harpalus* spp., were also more strongly associated with the agroforestry alleys than the arable fields, possibly because these carabids depend on local sources of seed food compared to predatory carabids (Woodcock et al. 2010).

Herbivorous invertebrates were more associated with the foliar domain in the agroforestry alleys, which could reflect the year-round availability of that domain in the agroforestry system, in contrast to the arable system. Natural enemies showed a different pattern, with the ground domain more associated with the agroforestry alleys, possibly explained by the more limited dispersal ability of ground-based predators. Exopterygotes (no pupal stage in the lifecycle) and partly or unwinged traits were also associated with the agroforestry alleys for both trophic levels, which could be explained in terms of dispersal ability. Poor dispersers, such as those without wings, respond more strongly to localized beneficial conditions because they experience their environment at a smaller scale compared to more mobile invertebrates (Tscharntke et al. 2005, 2007).

Therefore, we propose that invertebrate trait responses to farming system can be explained in terms of reduced disturbance and the availability of year-round vegetation. This is supported by previous findings of carabid beetle community trait differences between tree rows and crop alleys in agroforestry systems during winter (Boinot et al. 2019*b*). Taxonomic responses were less informative in our results. For example, the responses of ground beetles to farming system varied widely among species, which has been observed in other diversified farming systems (Varchola and Dunn 2001, Li et al. 2018, Jowett et al. 2019), probably because of the diversity of functional traits within this family.

The trait-based approach also had methodological advantages over a taxonomic-identity analysis. Multivariate pRDAs based on traits as response variables improved the variance explained by farming system, suggesting that this approach can detect a stronger signal with less noise than a taxonomic-identity approach. Therefore, the trait-based approach has potential methodological advantages in the study of agro-ecosystems and can improve the generality and mechanistic understanding of findings.

Diversity metrics: functional, taxonomic, and phylogenetic

Our finding of higher taxonomic richness and diversity in the agroforestry alleys compared to the arable fields is supported by previous findings in agricultural systems that have a lower management intensity (Attwood et al. 2008, Lichtenberg et al. 2017). We also found a stronger benefit to natural enemy Shannon and phylogenetic diversity early in the season, which suggests that agroforestry could play an important role for overwintering natural enemies. This is supported by the results of a previous study that investigated carabid beetles in an agroforestry system in France (Boinot et al. 2019*b*). We found weak but statistically significant spatial patterns in the agroforestry system, which suggests that the tree rows were driving the increased richness and diversity, but have far-reaching effects into the crop alleys.

Taxonomic diversity effect sizes decreased with increasing trophic level, which could be explained by the differing scales at which each trophic level experiences the surrounding landscape. Lower trophic levels are predicted to have smaller home ranges and dispersal ability and are therefore more influenced by local patch quality than landscape composition (Tscharntke et al. 2005). As such, the promotion of agroforestry systems to increase the biodiversity of higher trophic levels may only be achieved at large spatial scales.

Despite the lack of significant effects on Shannon diversity or phylogenetic diversity for natural enemies, functional trait diversity was significantly higher in the agroforestry crop alleys than the arable control fields. According to a meta-analysis of mesocosm studies, functional trait diversity of natural enemies is a stronger predictor of prey suppression than metrics based on taxonomic identity or phylogeny (Greenop et al. 2018). We would therefore recommend that consideration is given to the calculation of this metric in future studies of conservation biological control.

Pest suppression

The effect of farming system on pests and their natural enemies varied among taxa. For example, root flies were strongly suppressed in the agroforestry system at all three sites, but slugs were 39% more abundant in the agroforestry alleys than the arable fields, with a consistent effect across the two sites analyzed. Similar taxon dependency has been observed in responses to flower margins (Eggenschwiler et al. 2013, Tschumi et al. 2015). This highlights the limitations of attempting to infer pest control service by studying a single taxon, such as aphids, while crop rotation is also likely to be an important factor.

The natural enemy assemblages of each specific pest taxon can be expected to have many commonalities, particularly generalist predators such as spiders and many species of carabid and rove beetle. Therefore, the contrasting responses of pest taxa to farming system suggest that bottom-up habitat effects could drive pest suppression to a greater degree than top-down predation or parasitism.

Although the replications of pest taxa and sites in this study were inevitably limited, we hypothesize that pest suppression effects can be explained in terms of response traits, particularly resource attraction, mobility, and sensitivity to disturbance. For example, adult root flies and pollen beetles are highly mobile and attracted to freshly disturbed soil and flowers, respectively (AHDB 2015), both of which were more abundant in the arable than the agroforestry fields (for pollen beetles, when the arable crop was oilseed rape). Conversely, slugs are broad generalists, have limited mobility, and are sensitive to cultivation. Agroforestry systems provide year-round vegetation and refuges from cultivation, unlike arable systems, which could explain the greater abundance of slugs in agroforestry alleys than arable fields. This is a similar concept to the resource concentration hypothesis, which predicts that immigration of diet-specialist pests is higher, and emigration lower, in monocultures compared to polycultures (Root 1973). We therefore propose that agroforestry systems have different pest control issues than arable systems, based on the traits of those pests.

Caveats

Our approach was to rapidly characterize traits across plant and invertebrate communities, therefore some invertebrate traits could not be included in the analysis due to taxonomic resolution or a lack of literature. The study system is a rare, innovative design, which limited the availability of sites for replication. Nevertheless, all sites featured a pair of agroforestry and arable fields under identical management and in similar landscape contexts, while we sought to maximize within-site and temporal replication. The trait-based approach detected significant differences between farming systems and facilitated a mechanistic understanding of the effects, demonstrating the value of this approach even with limited replication among sites.

Site-level replication for plants and some pest taxa was further reduced because of the low coverage or abundance at some sites, which led to their exclusion from the analysis in some cases (Appendix S4). Therefore, further confirmation of the results, particularly for plants and invertebrate pest taxa, is recommended.

Previous studies have demonstrated benefits of grass and flower strips on natural enemy abundances and pest suppression (e.g., Collins et al. 2002, Hatt et al. 2017). As such, it is probable that the effects we find are primarily driven by the uncultivated strips of field-layer perennial vegetation rather than the trees themselves. Ideally, to disentangle the ecological effects of trees from uncultivated strips, this would be tested by comparing vegetation strips with and without trees. Nevertheless, the presence of productive trees provides an economic justification for a high density of ground vegetation strips within a field, compared to what would likely be tolerated by farm managers with treeless vegetation strips. Therefore, from an applied perspective, it is most appropriate to consider trees and ground vegetation strips in combination. At our study sites, the tree rows occupy approximately 10% of the agroforestry fields, which is far greater than typical densities of non-productive strips. For example, the recommended density of beetle banks in the UK is one per 16-ha field (Royal Society for the Protection of Birds 2017). In addition, the presence of trees is likely to increase the longevity of the permanent vegetation strips, because they offer a financial incentive for retention for the duration of their productivity.

The farms in our study were all ecologically managed to some extent. For example, at two of the three sites, arable field sizes were relatively small (~6 ha or less, Appendix S1) and set within well-wooded landscapes. Therefore, biodiversity could be expected to be relatively high, which could have masked effects relative to what would be expected from more intensively managed farms in simpler landscapes (Tscharntke et al. 2005, Fahrig et al. 2015, Jonsson et al. 2015, Staton et al. 2019). Furthermore, the agroforestry systems we studied were relatively recently established, which might have limited the colonization of new species compared to more established systems (Staton et al. 2019). Therefore, longer established systems in intensive landscapes could potentially achieve greater effects than we found in this study.

Comparisons between functional, taxonomic and phylogenetic diversity have been described as conceptually flawed on the basis that the latter two do not take traits into account, and therefore do not use comparable information (Mlambo 2014). We consider there is merit in making such a comparison, but careful interpretation is required. Our findings do not necessarily mean that taxonomic and functional traits are fundamentally different, as we do not account for taxonomic traits. Instead, we show that more consistent and statistically significant

patterns in the data can be detected by functional trait diversity rather than traditional taxonomic diversity metrics, such as Shannon diversity.

Conclusions

Our application of a trait-based approach to investigate the effect of farming system on functional biodiversity provided valuable insight into potential mechanisms behind the effects, which were consistent with reduced disturbance and the availability of year-round in-field vegetation in the agroforestry system. We found significantly higher functional trait diversity of natural enemies in agroforestry alleys vs. arable fields, but this was not detected by taxonomic diversity metrics. The taxon-dependent effects of farming system on pest abundance demonstrate the need to consider multiple taxa in studies of agricultural diversification on natural pest control. These effects were more easily explained by response traits rather than top-down control by natural enemies. This suggests that the effect of farming system on weeds and invertebrate pests could be predicted at any individual farm, i.e., annual, disturbance-tolerant weeds and specialist, highly mobile pests are predicted to be suppressed in agroforestry systems, in contrast to perennial weeds and generalist, low-mobility pests. We recommend validation and further application of trait-based approaches in future studies of agroforestry and other diversified farming systems.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2294/full

Data Availability

Data are available from the Dryad Digital Repository (Staton et al. 2020): https://doi.org/10.5061/dryad.rn8pk0p84.